

Learning to find fruit in *Ceratitis capitata* flies

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Abstract

Wild Mediterranean fruit fly females, *Ceratitis capitata* (Wiedemann), from an essentially monophagous population on the island of Hawaii were exposed to natural mock orange (*Murraya paniculata*) or sweet orange (*Citrus sinensis*) host fruit hung from branches of potted trees for 3-day periods in field enclosures. Subsequently, when flies were released individually onto potted trees harboring one or the other (or a mixture) of these fruit types, a higher proportion visited the type of fruit with which they were familiar (and visitors found familiar fruit faster) compared with the fruit type with which they were unfamiliar. Moreover, fruit-finding flies of this monophagous population attempted oviposition exclusively in the familiar fruit type, and thus appeared to be just as capable of learning to accept fruit for oviposition as wild flies from a previously-tested polyphagous population on the island of Maui. Additional tests were conducted in which flies were exposed to natural or colored-wax-covered mock oranges or sweet oranges and tested for response to colored-wax-covered natural or artificial fruit. Results suggested that fruit size was the principal character learned and used in finding mock orange or sweet orange fruit, while fruit color and odor appeared to be of little or no importance in this regard.

Introduction

Recently, in several phytophagous, saprophagous, and parasitoid insects, it has been shown that adult experience affects propensity to find food or egg-laying site resources and/or to utilize such resources upon arrival (reviewed in Papaj and Prokopy, 1989). In two tephritids, the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), and the apple maggot fly, *Rhagoletis pomonella* (Walsh), prior experience of mature females with host plant foliage appears to be of negligible biological significance (Prokopy *et al.*, 1989; Papaj & Prokopy, unpub. data). However, in both these species as well as in the

Queensland fruit fly, *Dacus tryoni* (Froggatt), studies have revealed that after a female alights on a host fruit, the propensity to accept (bore into) or reject that fruit for egg deposition is significantly modifiable according to prior ovipositional experience (Papaj *et al.*, 1987; Prokopy & Fletcher, 1987; Prokopy & Papaj, 1988).

Until now, there has been no investigation in tephritids of the effect of prior experience with host fruit on the propensity of females to alight on fruit of different species. In this study, using potted host trees in field cages, we asked first whether the propensity of medfly females to alight on two species of host fruit, mock orange (*Murraya paniculata*) and sweet orange (*Citrus*

sinensis), was influenced by previous experience with these fruit. After observing such an influence, we then asked what sorts of host fruit stimuli (odor or visual) were involved in modifying female responses to fruit. In addition to examining fruit-alighting propensity, we also recorded whether or not females accepted fruit after alighting.

Materials and methods

All medflies originated from larvae that infested field-collected fruit of unsprayed Jerusalem cherries, *Solanum pseudocapsicum*, taken from the southeastern slope of Mauna Loa volcano on the island of Hawaii. Upon eclosion, females were held together with males in cages without host fruit but supplied with water and food (3 × 6 cm strips of filter paper dipped in an aqueous slurry of yeast hydrolysate and sucrose and dried before use) under laboratory conditions at 25 °C, 80% RH and 13 h natural daylength.

For each experiment, ca. 80 female and 20 male mature medflies (12-15 days old) were transferred into each of 2 clear-nylon-screen exposure cages (1 m long × 1 m wide × 2 m tall) placed outdoors on the grounds of the USDA Tropical Fruit and Vegetable Research laboratory in Honolulu. The top of each cage was covered with a partly opaque tarpaulin to exclude direct sunlight and rainfall. A single non-fruiting potted guava tree, *Psidium guajava*, was placed 1 m above ground in the center of each cage. Each tree was ca. 70 cm in canopy diameter, 60 cm tall, and bore ca. 270 leaves. Before being used, the foliage and stems of each tree were rinsed thoroughly with water to remove any adhering substances. On each tree, we hung 4 aforementioned strips of food and 2 water vials with cotton wicks.

For Expts. 1-4, on Day 1, we hung on one tree 18 clusters (4 fruit/cluster) of fresh-picked, water-rinsed mock orange fruit. Each fruit was ca. 8 mm diam., orange-red in color, and punctured twice with a dissecting probe to facilitate entry of the ovipositor into the flesh. On the other tree on Day 1, we hung 4 water-rinsed sweet orange fruit, purchased from a local supermarket. Each was ca.

60 mm diam., orange in color, and punctured 36 times with a dissecting probe. In both cages, fruit were spaced evenly among the branches. Early on Day 3, the fruit in each cage were replaced with fresh specimens of the same type and number. On Day 4 (a test day), all but 5 clusters of mock oranges and all but 1 sweet orange were removed from the cages at 9 AM to circumvent over-depletion of female egg load while still providing a low level of available fruit. Removed fruit were returned to the cages at 4 PM but taken away again at 9 AM on Day 5 (also a test day).

For Expts. 5 and 6, procedures were the same as above except that all mock orange and sweet orange fruit in each exposure cage had been dipped either in orange- or green-dyed paraffin wax to alter fruit color while still maintaining fruit size and shape. We chose green dye in an attempt to approximate the color of such host fruit as limes, *Citrus medica*, which are green when susceptible to medfly oviposition. We chose orange dye in an attempt to approximate the color of such host fruit as sweet oranges. The wax coating was punctured with a probe, as before, to permit ovipositor entry into the flesh. Spectral reflectance curves of natural and dyed mock orange and sweet orange fruit as well as of lime fruit and guava leaves are given in Fig. 1.

On Days 4 and 5, females from both exposure cages were tested for propensity to alight upon and attempt oviposition into natural or waxed mock orange or sweet orange fruit or inanimate models of fruit. Tests were conducted in cylindrical 3.5 × 3.5 × 3 m clear-nylon-screen field cages. Each cage contained a single non-fruiting guava test tree of a size and leaf number equivalent to trees in the exposure cages. Each test tree was rinsed thoroughly before use. In Expts. 1, 5 and 6 (no-choice tests), we hung either 6 evenly-spaced clusters of natural or waxed mock oranges (2 fruit/cluster) or 2 natural or waxed sweet oranges on each test tree. None of the fruit was punctured with a probe. Expt. 2 (choice test) was similar to Expt. 1 except we hung 6 clusters (2 fruit/cluster) of mock oranges plus 2 sweet oranges on each tree. In Expt. 3 (no-choice test) and Expt. 4 (choice test), test 'fruit' consisted of

6 clusters of 8-mm-diam plastic spheres (2 spheres/cluster) and/or 2 60-mm-diam plastic spheres. All spheres were dipped in green-dyed paraffin before use.

For testing females, a fruit of the same type to which a female had been exposed was attached to a dissecting probe and held in the canopy of an exposure tree until a female alighted on it and commenced boring. During boring, the female and fruit were moved gently to the test cage, where the fore-tarsi of the still-boring female were nudged onto the upper surface of a leaf at the lower center of the plant canopy. After boring, the female walked readily onto the leaf surface. We adopted this procedure to standardize as much as possible the physiological state of released females. To ensure uniformity of procedure, females were always released onto the same leaf of a test tree. Females that did not leave the release leaf within 5 min were disqualified. We monitored the duration of time the female spent on the test tree since leaving the release leaf until it visited a fruit, left the tree without visiting a fruit (= non-finder), or 10 min elapsed without visiting a fruit (= non-finder). If a female alighted on a fruit, we monitored whether she bored, left the fruit without boring (= non-borer), or 5 min elapsed without boring (= non-borer). To minimize experimental error, we alternated fly exposure and test fruit treatments in a carefully controlled systematic fashion. All tests were conducted in March, 1988.

Results

The results (Table 1) show that in Expt. 1 (no-choice test), significantly more flies exposed to natural mock oranges (84%) than to natural sweet oranges (19%) alighted on natural mock oranges, while significantly more flies exposed to natural sweet oranges (78%) than to natural mock oranges (50%) alighted on natural sweet oranges. Mock oranges were found significantly faster by mock-orange-exposed than by sweet-orange-exposed flies. Sweet oranges were found significantly faster by sweet-orange-exposed than

by mock-orange-exposed flies. Finally, 100% of arriving mock-orange-exposed but 0% of arriving sweet-orange-exposed flies accepted mock oranges for oviposition (a significant difference), whereas 84% of arriving sweet-orange-exposed but 0% of arriving mock-orange-exposed flies accepted sweet oranges for oviposition (a significant difference). The exposure and test fruit in Expt. 2 (choice test) were the same as in Expt. 1. Again, significantly more mock-orange-exposed than sweet-orange-exposed flies alighted on mock oranges (50 vs. 9%), while significantly more sweet-orange-exposed than mock-orange-exposed flies alighted on sweet oranges (68 vs. 32%).

Expt. 3 (no-choice test) was aimed at determining whether the difference in fruit size between mock oranges (8 mm) and sweet oranges (60 mm) contributed to the pattern of results in Expts. 1 and 2. The use of inanimate models in place of real test fruit and the coating of models with green wax were intended to eliminate odor and color differences between mock oranges and sweet oranges as variables. The results show that significantly more flies exposed to natural mock oranges (88%) than to natural sweet oranges (50%) alighted on 8 mm green waxed spheres. Conversely, significantly more flies exposed to natural sweet oranges (84%) than to natural mock

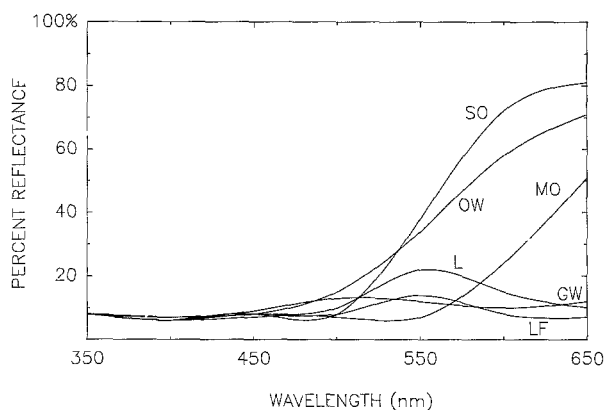


Fig. 1. Spectral reflectance of guava leaves (LF), natural mock oranges (MO), natural sweet oranges (SO), natural limes (L), green-dyed paraffin wax (GW), and orange-dyed paraffin wax (OW).

Table 1. Following 3 days of exposure to natural or colored-wax-covered mock orange (MO) or sweet orange (SO) fruit, percent of assayed *C. capitata* females arriving on test fruit, time from release until arrival, and percent of arriving females accepting test fruit for oviposition

Pre-test Experience				Test Results					
Expt.	♀ ♀ exposed to	Approx. total no. eggs laid in fruit during 3-day exposure period	N ²	% ♀ arriving on test fruit ¹		Mean time from release to arrival on fruit (sec) ¹		% arriving ♀ accepting test fruit ¹	
1				Natural MO	Natural SO	Natural MO	Natural SO	Natural MO	Natural SO
no-choice	Natural MO	2,400	32	84a	50b	47a	70b	100a	0b
test	Natural SO	3,500	32	19c	78a	123b	43a	0b	84a
2				Natural MO	Natural SO	Natural MO	Natural SO	Natural MO	Natural SO
choice	Natural MO	–	22	50ab	32bc	37a	66a	–	–
test	Natural SO	–	22	9c	68a	89a	46a	–	–
3				Green waxed spheres MO size	Green waxed spheres SO size	Green waxed spheres MO size	Green waxed spheres SO size	Green waxed spheres MO size	Green waxed spheres SO size
no-choice	Natural MO	1,500	32	88a	63b	47a	79b	54a	5b
test	Natural SO	1,000	32	50b	84a	52ab	34a	0b	15b
4				Green waxed spheres MO size	Green waxed spheres SO size	Green waxed spheres MO size	Green waxed spheres SO size	Green waxed spheres MO size	Green waxed spheres SO size
choice	Natural MO	–	22	55a	23b	51a	84a	–	–
test	Natural SO	–	22	13b	63a	81a	40a	–	–
5				Green waxed MO	Orange waxed MO	Natu- ral MO	Green waxed MO	Orange waxed MO	Natu- ral MO
no-choice	Green- waxed MO	700	32	72a	63a	69a	60a	65a	65a
test	Orange- waxed MO	800	32	69a	66a	59a	53a	80a	47a
6				Green waxed SO	Orange waxed SO	Green waxed SO	Orange waxed SO	Green waxed SO	Orange waxed SO
no-choice	Green- waxed SO	3,800	32	75a	68a		16a	11a	
test	Orange- waxed SO	3,600	32	59a	75a		13a	12a	

¹ Values in each experiment followed by same letter not significantly different at 0.05 level using G-tests (for % arrivers or acceptors) or Mann-Whitney U tests (for time to arrival).

² No. females released on test tree.

oranges (63%) alighted on 60 mm green waxed spheres. Among alighting flies, 8 mm models were found slightly but not significantly faster by mock-orange-exposed than by sweet-orange-exposed flies, while 60 mm models were found significantly faster by sweet-orange-exposed than by mock-orange-exposed flies. Finally, 54% of arriving mock-orange-exposed but 0% of arriving sweet-orange-exposed flies accepted 8 mm models for oviposition (a significant difference), whereas 15% of arriving sweet-orange-exposed compared with 5% of arriving mock-orange-exposed flies accepted 60 mm models for oviposition (not a significant difference). The exposure and test fruit in Expt. 4 (choice test) were the same as in Expt. 3. Again, significantly more mock-orange-exposed than sweet-orange-exposed flies alighted on 8 mm models (55 vs. 13%), and significantly more sweet-orange-exposed than mock-orange-exposed flies (63 vs. 23%) alighted on 60 mm models.

The intent of Expts. 5 and 6 (no-choice tests) was to assess whether exposure of females to different colors of waxed fruit affected propensity to alight on or, after alighting, to accept differently colored waxed or natural fruit (Fig. 1). Irrespective of whether exposure fruit were green- or orange-waxed mock oranges and test fruit were of these 2 sorts or natural mock oranges (Expt. 5), and irrespective of whether exposure and test fruit were green- or orange-waxed sweet oranges (Expt. 6), no significant effects of prior experience with green-colored vs orange-colored fruit were found.

Discussion

Our findings from Expts. 1 and 2 demonstrate that the propensity of medfly females to alight on natural mock orange or natural sweet orange host fruit hung in trees in field cages is affected significantly by the nature of their prior experience with these fruit types. Thus, a higher proportion of flies visited the type of fruit with which they were familiar than the type with which they were unfamiliar. In addition, among flies visiting fruit,

familiar fruit was found faster than unfamiliar fruit.

A rigorous, all-encompassing definition of animal learning is elusive. Nonetheless, according to several properties characteristic of learning put forward in Papaj and Prokopy (1989), it would appear from our experiments that medfly females are indeed capable of learning to find fruit in a host tree, just as they are able to learn to accept or reject fruit for oviposition.

In studies reported to date on post-alighting, fruit-acceptance learning in medflies (Cooley *et al.*, 1986; Papaj *et al.*, 1987, 1989), all wild flies tested originated from a population in the Kula area of the island of Maui that annually used a succession of hosts, primarily loquats, peaches, figs and citrus. In contrast, the population tested here from the island of Hawaii appears to have been, for tens and perhaps even hundreds of generations, essentially monophagous on Jerusalem cherries (R.T. Cunningham, pers. communication). In previous tests comparing ovipositional responses of flies from each of these populations to an array of host fruit, naive females from the Jerusalem cherry population on Hawaii were found to accept mock oranges to a significantly greater degree than did naive females from the mixed-host population on Maui (Prokopy *et al.*, 1984). Both accepted large citrus fruit (sweet oranges and grapefruit) to an approximately equal degree.

Our findings here indicate that females from the Jerusalem cherry population on Hawaii are no less capable of learning to accept or reject mock oranges or sweet oranges for oviposition than are females from the previously-tested mixed-host population on Maui. In the only other studies of which we are aware comparing host learning ability in different wild populations of conspecific phytophagous insects, no differences were detected between populations of *R. pomonella* flies originating from hawthorn or apple in Massachusetts (Prokopy *et al.*, 1986) or between populations of *Battus philenor* L. butterflies originating from 2 *Aristolochia* hosts in East Texas or a single *Aristolochia* host in Virginia (Papaj, 1986a). Significant differences in fruit-acceptance

learning ability between a laboratory-cultured population and wild medflies of the mixed-host population on Maui have been detected, however (Papaj *et al.*, 1987).

In assays of medfly (Maui origin) ovipositional responses to mock oranges and sweet oranges immediately following laboratory-cage exposure to one or the other of these fruit types for 3 days, Cooley *et al.* (1986) and Papaj *et al.* (1987) reported very high acceptance of the familiar fruit type and high but not absolute rejection of the unfamiliar fruit type. Here, following 3 days of exposure of medflies (Hawaii origin) to these same fruit types on trees in field cages, acceptance of the familiar fruit type likewise was very high while rejection of the unfamiliar type was absolute. This suggests that future investigations conducted under semi-natural (field-cage) rather than laboratory conditions might be more rewarding when examining effects of learning on medfly acceptance of fruit for oviposition.

The levels at which unfamiliar natural mock orange and sweet orange fruit were rejected for oviposition here were substantially greater than the levels at which unfamiliar fruit of these types went unfound by foraging females. This suggests that prior experience of a medfly with a particular type of host fruit may have a less profound effect on the propensity of that fly to find other types of fruit than on its propensity to oviposit in other types of fruit after arrival. The same appears to be true in *R. pomonella* (Prokopy *et al.*, unpub. data).

During host finding in other phytophagous insects, prior experience with hosts enhances upwind response to host plant odor in *Leptinotarsa* beetles (Visser & Thiery, 1986) and *Schistocerca* nymphs (Lee *et al.*, 1987). *Heliconius* and *Pieris* butterflies learn color/light intensity cues in finding nectar sources or egg-laying sites (Swihart & Swihart, 1970; Traynier, 1986; Lewis & Lipani, 1989), as do *Melanoplus* nymphs in finding food (Bernays & Wrubel, 1985). Ovipositing *Battus* butterflies find suitable hosts sometimes by learning the shape of host leaves and sometimes by learning visual cues associated with the terminal leaf bud (Papaj 1986a,b,c).

Here, evidence from Expts. 3-6, in which

medflies were exposed to natural or colored-wax-covered mock oranges or sweet oranges and tested for response to colored-wax-covered natural or artificial fruit, suggests that fruit size was the principal character learned and used by medflies in finding familiar mock oranges or sweet oranges. Fruit color and fruit odor appeared to be of lesser, if any, importance. It should be noted, however, that while we have in the past been able to mimic closely reflectance patterns of plant leaves and fruit using mixtures of artist pigments (Prokopy & Owens, 1986), we were unable here to mimic closely fruit reflectance patterns with mixtures of candle wax dyes. Although the green-dyed and the orange-dyed waxed 'fruit' were distinctly different from one another in hue and intensity of reflection (Fig. 1), as were natural lime and sweet orange (or mock orange) fruit, medflies may not have responded to differences in reflectance patterns of the dyed fruits in the same fashion as they might to differences in reflectance patterns of real fruit. The degree to which fruit size, as opposed to fruit color or odor, might affect medfly ability to learn to find fruit of types other than mock oranges or sweet oranges remains to be determined. Interestingly, fruit size as well as fruit chemical stimuli are both important in medfly fruit-acceptance learning following arrival on fruit (Papaj *et al.*, 1989).

Does learning of host fruit characters by medfly females have any practical implications for pest management programs? At this point, one can only speculate. However, simultaneous availability of multiple host fruit types in the same habitat is not uncommon in this highly polyphagous species. Conceivably, substantial ovipositional experience of medflies with a particular species of fruit could influence fly propensity to exploit that species to the partial or complete exclusion of other rewarding (but unfamiliar) host fruit in the habitat. If that particular species became unusable owing to fruit drop or fruit stripping (as in population suppression programs – Jackson & Lee, 1985), considerable (long-distance) movement of flies in search of that species could ensue. Fly monitoring and management practices would have to be adjusted accordingly.

Résumé

L'apprentissage de la découverte des fruits par Ceratitis capitata

Des femelles sauvages d'une population essentiellement monophage de *C. capitata* Wiedemann, provenant de l'île de Hawaï, ont été mises en présence pendant des périodes de 3 jours dans des enceintes dans la nature à des fruits de *Murraya paniculata* et de *Citrus sinensis* suspendus à des branches d'arbres empotés. Quand les mouches ont été libérées individuellement sur les arbres empotés portant l'un ou l'autre de ces fruits (ou leur mélange), une plus forte proportion a visité le fruit avec lequel elles étaient familiarisées (et l'ont trouvé plus vite) que le fruit avec lequel elles ne n'étaient pas. De plus, les femelles découvrant des fruits de cette population monophage ne tentèrent de pondre que dans le type de fruit avec lequel elle étaient familiarisées. Elles se montrèrent aussi capables que les mouches d'une population polyphage de l'île de Maui d'apprendre à accepter de nouveaux fruits pour pondre. Des expériences complémentaires ont été réalisées dans lesquelles les mouches étaient mises en présence de fruits de *M. paniculata* ou de *C. sinensis* naturels ou couverts de cire colorée ou encore de fruits artificiels. Les résultats suggèrent que la taille du fruit est le principal critère d'apprentissage utilisé pour trouver *M. paniculata* ou *C. sinensis*, la couleur et l'odeur du fruit étant apparus comme de moindre importance ou sans effet.

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